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Geographic Variation in Naupliar Growth and Survival in a Harpacticoid Copepod

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Abstract. Newly hatched nauplii of *Scottolana canadensis* (Willey) collected from two locales in Maine were larger than Maryland nauplii when females were reared under identical conditions (20°C and high food concentration, 2.5×10^5 algal cells ml^{-1}). Under high food concentration, Maryland nauplii had faster growth rates ($\log_{10} \mu m\ h^{-1}$) than Maine nauplii, but survivorship was similar. Growth rates were lower under low food concentration (0.5×10^5 cells ml^{-1}), and were the same for all locales, whereas survivorship of the Maine nauplii through NV was higher than the Maryland nauplii. We hypothesize that size-related differences in naupliar feeding efficiency may explain the variation in survival under low food stress.

Introduction

In many marine organisms with mechanisms for dispersal and hence the potential for gene flow, genetic differentiation of populations has occurred (*e.g.*, as found in copepods; Bucklin and Marcus, 1985; Burton, 1986; reviewed in Hedgecock, 1986). The potential for genetic differentiation of estuarine populations may be greater than that for coastal populations because of physical barriers to dispersal (*e.g.*, salinity and temperature; Koehn *et al.*, 1980; McAlice, 1981) and because selective forces arising from human activities may be more intense (*e.g.*, PCB pollution; Cosper *et al.*, 1984, 1988; see review by Levinton, 1980).

Scottolana canadensis (Willey; but see Por, 1984) is a widespread, brackish-water harpacticoid copepod (Willey, 1923; Haertel *et al.*, 1969; Coull, 1972). When common-rearing techniques were used in the laboratory, females from Maine (43°N) produced larger eggs that took longer to develop at all test temperatures than those from Maryland (38°N) and Florida (27°N; Lonsdale and Levinton, 1985a). These results were contrary to the expectation that northern-derived populations would demonstrate compensation for low temperature. Furthermore, low food stress (2.5×10^4 algal cells ml^{-1}) produced locale differences in newborn survival, with Maine nauplii surviving in the highest proportion. Although variation in egg size does not necessarily reflect differences in egg organic content (McEdward and Carson, 1987), the correspondance between large egg size and increased survival of newborns suggested that the Maine females produced eggs with more yolk than did females from other locales, resulting in differences in maternal reserves for newly hatched nauplii (Lonsdale and Levinton, 1985a).

The Saco River, from which the Maine *S. canadensis* individuals were collected, is characterized by extremely high rates of freshwater flow (B. McAlice, pers. comm.), and Saco Bay receives "sediment input grossly out of proportion to (its) size" (Kelly *et al.*, 1986; cited in Jacobson *et al.*, 1987). The planktonic nauplii of *S. canadensis* would probably reach their physiological limits once carried into the Gulf of Maine due to rapidly declining temperatures (McAlice, 1981) and possibly to increased salinities. Laboratory studies have shown that the survivorship of *S. canadensis* is adversely affected by higher salinities (responses to 10, 15, and 20‰ were studied; Lonsdale, 1981), but the differences were largely found in the epibenthic copepodites rather than the planktonic nauplii. Thus, the efficacy of salinity as a barrier to dispersal in the species is moot.

In this paper, we present the results of a test of the "nauplius development time restriction" hypothesis; *i.e.*, that "yolkier eggs may enhance the rate of nauplius development to Copepodite I, at which stage they migrate

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Table I

Location and physical characteristics of collection sites for Scottolana canadensis

Collection site	Date	Temperature (°C)	Salinity (‰)
Sheepscott River (SHP), Wiscasset, Maine	May 1988	17	12
Saco River (SR), Biddeford, Maine	May 1988	13	10
Patuxent River (MD), Lusby, Maryland	May 1988	18	10

to the bottom, thereby increasing the probability of *S. canadensis* remaining within the (Saco River) estuary" (p. 428; Lonsdale and Levinton, 1985a). Thus, the egg and naupliar traits of the Maine copepods may not have reflected a latitudinal trend, but rather a localized evolution to a unique hydrodynamic condition. To test the hypothesis, we compared egg development time, egg size, and naupliar growth and survival rates of *S. canadensis* collected from the Saco River (SR) and Sheepscott River (SHP) estuaries in Maine, and the Patuxent River estuary in Maryland (MD).

Materials and Methods

Field collections

Planktonic nauplii of *Scottolana canadensis* were obtained with a 63 μm-mesh net from three sites on the east coast of North America; pertinent collection information is listed in Table I. Separate collections consisted of 250 or more nauplii. Specimens of *Scottolana* collected from Maine and Maryland are interfertile (Lonsdale *et al.*, 1988).

Culture methods

In the laboratory, wild-caught copepods were cultured at 20°C in 1000-ml Erlenmeyer flasks containing 15‰ seawater. Seawater was prepared with water from Stony Brook Harbor, New York (~27 ‰), adjusted to 15‰ with distilled water, filtered through 20-μm mesh, and autoclaved. Algae also were cultured at 20°C and 15‰ with a 14:10 hour light-dark cycle in f/2 enrichment medium (Guillard, 1975), and maintained in an approximately log phase of growth by harvesting and adding medium three times weekly. Generally, algal cultures used both in copepod culturing and experiments ranged in age from 5 to 14 days. Cell densities were assessed with a hemocytometer. A mixture of two algal species—*Isochrysis galbana* (ISO; ~4–6 μm diameter and ~14.1 pg C cell^{-1} according to the Strathmann equations; Strathmann, 1967) and *Thalassiosira pseudonana* (3H; ~4 μm and ~9.0 pg C cell^{-1})—was added to each copepod culture three times weekly to produce a minimum density of 2.5×10^5 cells ml^{-1}. Copepod batch cultures from each locale (SHP, SR, MD) were maintained for at least two months prior to experimentation.

Experimental procedures

Egg development times. Seventy-five nauplii (all stages) from each locale were removed from batch culture and reared in 1000-ml beakers using the above methods. These and all other experiments were conducted at 20°C. At this temperature, copepods from Maine and Maryland exhibited little difference, either in mean growth rate from naupliius I to adult, or in adult female energy budgets (Lonsdale and Levinton, 1985b, 1986, 1989). Several additional cultures of SHP nauplii were set up because the first had produced many nonreproducing females, possibly due to an infectious agent (see Lonsdale and Levinton, 1986).

Following maturation, up to 30 gravid females were selected and individually placed in 50-ml covered Stendor dishes. Each dish contained about 20 ml of sterilized seawater to which algae (a 1:1 mixture by cell number of *I. galbana* and *T. pseudonana*) was added to bring the food concentration to 2.5×10^5 cells ml^{-1}. Females were fed three times weekly, and the seawater was changed once a week. To further minimize culture effects on egg traits, development times were determined only after the female produced a second or third clutch. The third clutch was studied in the case of females already carrying egg sacs. Usually, these females were producing additional eggs visible in the oviducts.

To estimate egg development times, observations were made at 4-h intervals. Total time (h) was calculated from the extrusion of eggs in sacs, to naupliar hatching.

Egg volume. To determine whether females collected from the Saco River estuary produced larger eggs than those from the Sheepscott River and Patuxent River estuaries, females with egg clutches were preserved according to the procedures outlined by Gallager and Mann (1981). To determine whether changes in egg volume are associated with embryogenesis, some females were preserved within 4 h of clutch formation (t = 0 h) and others after 24, 48, 72, or 96 h (for each locale and time condition, n = 3–4 females except n = 2 for SHP at 96 h due to the low number of fecund females). For each clutch, dimension measurements were made on six eggs. Egg volume was calculated (after Allan, 1984) according to the formula: volume (μm^3) = $\frac{4}{3} \pi r_1 r_2^2$, where r_1 and r_2 are the radii of the long and short dimensions, respectively. Egg dimensions and lengths of females (μm) were measured with an Optical Pattern Recognition System

Table II

Mean (95% confidence interval) CI length (μm) and total development time (h) to CI for Scottolana canadensis *collected from three locales (SR, SHP, and MD) and reared at 20°C and two food concentrations (2.5 and 0.5 × 10^5 cells ml^{-1})*

Food	Locale	Length	Development time
2.5	SR	341 (330–352)	112 (106–118)
	SHP	329 (318–341)	112 (105–120)
	MD	313 (302–324)	103 (96–111)
0.5	SR	308 (301–316)	164 (135–201)
	SHP	297 (268–329)	163 (136–195)
	MD	293 (278–309)	141 (110–180)

SR = Saco River; SHP = Sheepscott River; MD = Patuxent River.

(Biosonics, Inc.) at 400 × enlargement under a Zeiss compound microscope. Female dry mass was estimated by the equation: $Y = 8.415\ X^{1.957}$, where Y = μg dry mass, and X = length in mm (Lonsdale and Levinton, 1985b).

Naupliar growth and survival. Newborn nauplii, obtained from the egg development time studies, were placed individually in wells of a multi-depression dish that was contained within an airtight opaque plastic box. Distilled water in the bottom of the box reduced evaporation from the wells. Four sibs from five (SHP) or six families (SR, MD) were followed at each food concentration (0.5 and 2.5 × 10^5 cells ml^{-1}). The carbon concentration of the algal suspensions (~577 and 2887 μg $C\ l^{-1}$, respectively) were within the range found in many estuaries (*e.g.*, 240–3910 μg $C\ l^{-1}$ for East Lagoon, Texas (Ambler, 1986) and 500–3388 μg $C\ l^{-1}$ for Narragansett Bay (Durbin *et al.*, 1983). Six additional sibs were preserved in 5% buffered formalin for measurements of body dimensions (length and width) that were determined at 100× enlargement with a Wild inverted microscope. (Nauplii from one SHP family were inadvertently not sampled for measurement.) The algal suspensions in the wells were completely replaced daily at 1200 h, and a 50% replacement occurred at 2400 h. The algal suspensions were prepared fresh each day from sterilized, filtered seawater (15‰) and algae. The copepods were observed about every 4 h, and the time to each stage (NII to CI) was noted. Molt lengths were measured during the 100% medium replacement.

Equality of variances in the data sets was tested using the F_{max}-test and, if necessary, the data were $\log_{10}$ transformed prior to analysis of variance (Sokal and Rohlf, 1981). Most statistical tests were conducted using the packages of Sokal and Rohlf (1981) or SAS.

Results

Egg development time

A significant difference in egg development time was found among locales (One-way ANOVA; df = 2,27, F = 17.03, $P < 0.0001$). Mean egg development time (95% confidence interval) of MD females was significantly less than that of SR and SHP females [74.1 (72.3–75.9) h *versus* 99.2 (93.9–104.5) and 98.0 (81.4–114.6) h, respectively; 5% critical value, Tukey-Kramer method for unplanned comparisons among means]. There was no significant difference in development time among the Maine eggs. Mean egg development times were very similar to those previously obtained at 20°C (97.3 and 70.4 h for SR and MD locales, respectively; see Table II, Lonsdale and Levinton, 1985a).

Egg size

Mean egg volume of a clutch (μm^3) was not significantly affected by total incubation time (0 to 72 h for MD and 0 to 96 h for SR and SHP), as the regression equations were not significant for several models tested (*e.g.*, linear, $P > 0.5$, 0.1, and 0.1, respectively). Thus, the incubation time series data were pooled by collection locale. Both locale and family within locale influenced egg volume (Nested ANOVA using $\log_{10}$ transformed data sets; df = 2,217, F = 44.94, $P < 0.001$ and df = 41,217, F = 5.99, $P < 0.001$, respectively; Fig. 1). MD females produced significantly smaller eggs than either SR or SHP females [6.18 (5.75–6.64) × 10^4 μm^3 *versus* 8.37 (7.91–8.86) and 8.09 (7.59–8.62) × 10^4 μm^3, respectively] and there was no difference between the latter two locales (5% critical value, Tukey-Kramer method).

The mean dry mass of females was 8.2 (7.2–9.2), 9.1 (8.3–9.9), and 7.4 (6.7–8.1) μg for MD, SR, and SHP, respectively. Differences in dry mass did not account for the locale effects on egg volume (ANCOVA for dry mass

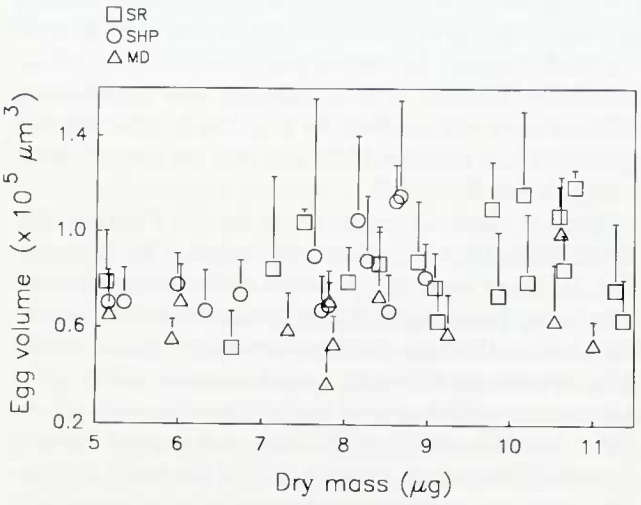

Figure 1. Mean egg volume (+95% confidence interval) and dry mass of females of *Scottolana canadensis* collected from three locales [Saco River (SR), Sheepscott River (SHP), and Patuxent River (MD)] and reared at 20°C and 2.5 × 10^5 cells ml^{-1}.

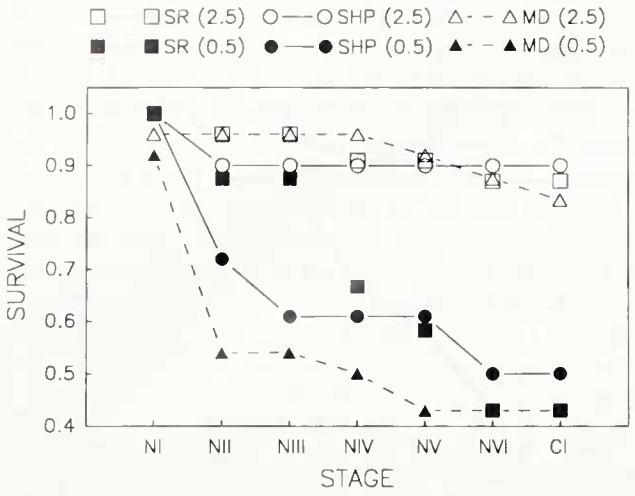

Figure 2. Survival of *Scottolana canadensis* at each naupliar stage when reared at 20°C and at concentrations of 2.5 and 0.5 × 10^5 cells ml^{-1}.

adjusted volumes; df = 2,257, F = 21.24, $P < 0.001$, Fig. 1).

Naupliar newborn size, survivorship, and growth rate

The length (μm) of newborn nauplii was influenced by both locale and family within locale effects (Nested ANOVA using $\log_{10}$ transformed data sets; df = 2,78, F = 11.45, $P < 0.001$ and df = 15,78, F = 2.46, $P < 0.01$, respectively). MD newborns were significantly smaller than those from SHP and SR, and there was no difference among the latter two groups [91 (90–92) μm *versus* 99 (98–101) and 100 (99–101) μm length, respectively; 5% critical value, Tukey-Kramer method]. Similarly, locale and family within locale were significant factors affecting maximum head width (Nested ANOVA; df = 2,78, F = 42.96, $P < 0.001$ and df = 15,78, F = 4.11, $P < 0.001$, respectively). All locales were significantly different from one another [54 (53–55), 57 (56–59), and 61 (60–63) μm for MD, SHP, and SR; 5% critical value, Tukey-Kramer method].

Naupliar survival was poorer at the low food concentration than at the high food concentration for all locales (Fig. 2). There were no significant differences among locales in the proportion of nauplii surviving through the NV stage at the high food concentration (paired t-test using arcsine transformed proportions of survivors at each stage; df = 4, $t_s = 0.913$, $P > 0.4$ in a comparison of SHP *versus* SR, and $t_s = 0.112$, $P > 0.9$ in a comparison of pooled Maine data *versus* MD). At the low food concentration, no significant difference in survivorship was found among SR and SHP nauplii ($t_s = 0.755$, $P > 0.5$), but the survival of MD nauplii was significantly less than that of Maine nauplii ($t_s = 3.733$, $P < 0.05$). The survival advantage of Maine nauplii was lost during the NVI stage (Fig. 2).

Molt lengths of MD nauplii were in general shorter than those of Maine *S. canadensis* (Fig. 3). The molt length of CI copepodites was affected by collection locale and by food concentration (Two-way ANOVA using $\log_{10}$ transformed data sets; df = 2,74, F = 6.73, $P < 0.01$ and df = 1,74, F = 25.50, $P < 0.0001$, respectively; Table II. The influence of family within locale was not investigated because some families had no CI survivors at the low food concentration). The low food concentration resulted in smaller copepodites, and those from MD were smaller at the high food concentration than either SR or SHP copepodites (5% critical value, Tukey-Kramer method). At the low food concentration, the molt lengths of the copepodites collected from different locales were not significantly different.

The low food concentration also resulted in a longer total development time (h) to CI (Two-way ANOVA us-

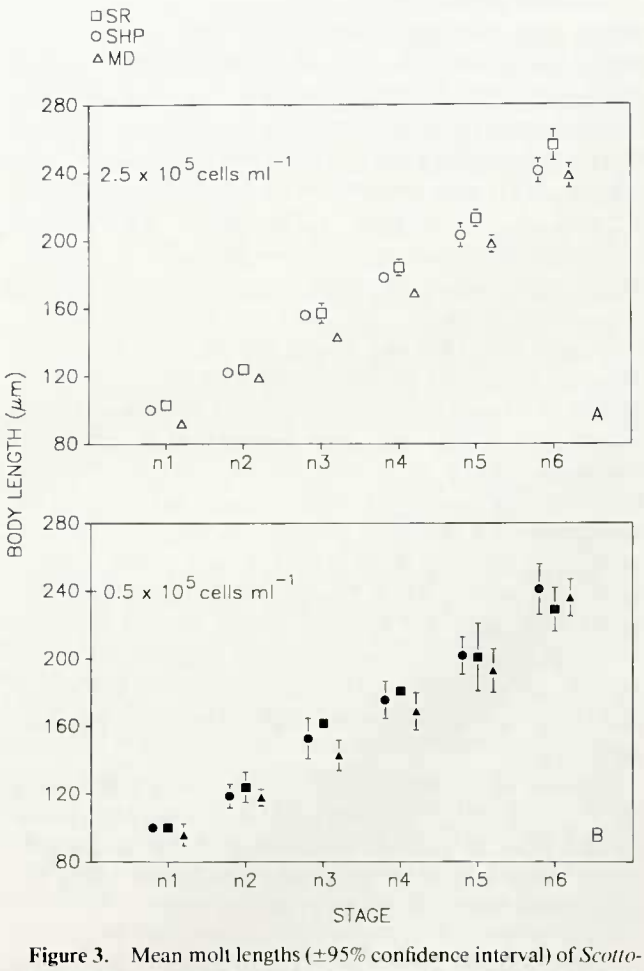

Figure 3. Mean molt lengths (±95% confidence interval) of *Scottolana canadensis* nauplii collected from three locales [Saco River (SR), Sheepscott River (SHP), and Patuxent River (MD)] and reared at 20°C and either 2.5 or 0.5 × 10^5 cells ml^{-1}. Missing confidence intervals are smaller than the height of the symbol.

ing $\log_{10}$ transformed data sets; df = 1,79, F = 62.00, $P < 0.0001$; Table II) and although MD nauplii had a shorter mean development time at both food concentrations, locale variation was marginally not significant (df = 2,79, F = 3.03, $P = 0.054$).

Regressions of molt length (log transformed) *versus* total development time were significant for all of the growth rate studies ($P < 0.001$ for all regressions; Fig. 4). At the high food concentration, the regression coefficient for MD was significantly higher than either SR or SHP, and the latter two were not different from one another (Tukey-Kramer method for unplanned comparisons among a set of regression coefficients using 5% critical values). However, there were no significant locale differences among regression coefficients at the low food concentration, and all those coefficients were significantly lower than the ones obtained under the high food concentration.

Discussion

Our results did not support the "nauplius development time restriction" hypothesis (Lonsdale and Levinton, 1985a). Total development time to CI was not less for SR nauplii than for those from either MD or SHP at either food concentration. *Scottolana* from the Saco River estuary were also similar to copepods from the Sheepscott River estuary in other life-history traits, such as egg development time, egg volume, and newborn size. This research, therefore, provides more evidence for genetically based, latitudinal differences in life-history traits of *S. canadensis* (between Maine and Maryland).

The adaptive significance of latitudinally related variation in newborn size in *S. canadensis* remains unclear and may, in fact, be due to genetic drift of isolated populations (see Hines, 1986, and Slatkin, 1987, for general reviews). On the other hand, the attainment of a larger newborn size appears to encumber a fitness cost in terms of prolongation of embryogenesis. In turn, this cost may be offset by the survival advantages of a larger body size. For example, the predation rate of the adult copepod *Acartia tonsa* on copepod nauplii was inversely related to naupliar body size (when NI-III and NIV-VI were compared), although prey swimming ability and behavior also may have been important (Lonsdale *et al.*, 1979; Tackx and Polk, 1982). In MD, however, invertebrate predation is an important regulator of *S. canadensis* population growth (Lonsdale, 1981), and thus, the laboratory differences in naupliar size *per se* are not likely a reflection of habitat variation in this selective pressure.

We suggest an additional fitness advantage of larger body size. A preliminary examination of eggs preserved within 4 h of mean hatching time (72 h for MD copepods and 96 h for Maine) revealed that the total lipid staining area (μm^2 using Oil Red O; Gallager and Mann, 1981) of the eggs was not different among locales [62 (11–113), 89 (19–159), and 112 (−32–256) μm^2 for MD, SR, and SHP, respectively)]. Although these area measurements are not an optimal estimate of lipid content (Gallager and Mann, 1986), they do suggest that variation in maternal reserves did not contribute to the survival differences of the nauplii under low food stress. Thus, there may have been size-related differences in naupliar feeding efficiency (energy ingested–energy expended; Hall *et al.*, 1976; Sebens, 1982). Larger body size may result in a greater filtering capacity (per animal), or greater difference between weight-specific energy acquisition and expenditure, as compared to smaller forms (Hall *et al.*, 1976; Gliwicz, 1990). The survival patterns of *S. canadensis* may indicate that under the high food concentration, differences were not found because the energetic demands of growth were met for both MD and Maine nauplii. But under the low food concentration, the energetic impact of lower feeding efficiency resulted in higher mortality of the MD copepods. The survival advantage of Maine nauplii was lost during the NVI stage, perhaps for several reasons. First, at NVI, the molt lengths of the Maine and MD nauplii were similar (Fig. 3B) and thus, there would be no size-related advantage. Second, the metamorphosis of *S. canadensis* nauplii to copepodites was associated with the highest stage-specific growth rate ($\mu m\ h^{-1}$) compared to all other stages of nauplii and required substantial morphological change.

In previous studies, the mean growth rate (μg dry mass d^{-1}) of SR and MD females was usually not different, particularly at 20°C, nor were the components of growth rate (*i.e.*, adult dry mass and total time from NI to the adult molt; Lonsdale and Levinton, 1985b, 1986). Yet growth rate differences during the naupliar stages have been shown in this study. However, in this study, the growth rates of SR and MD female copepodites (CI to adult molt) were similar [$\log Y = 2.35 + 0.00187$ (± 0.00023) X and $\log Y = 2.32 + 0.00195$ (± 0.00036) X where Y = μm and X = h, respectively and at the high food concentration; unpubl.]. This result may help explain the lack of concordance between mean growth rate to adult and naupliar growth rate with regard to the influence of collection locale.

The egg volumes determined in this study were ~25–30% less than those reported by Lonsdale and Levinton (1985a) for both the Maine and MD locales. This discrepancy may be due to differences in the preservation process; in the previous study copepods were not narcotized with $MgCl_2$ prior to preservation in formalin. Initial estimates of egg volumes of Maine *S. canadensis* individuals collected from the field, and which were not narcotized prior to formalin preservation, were more similar to those reported by Lonsdale and Levinton

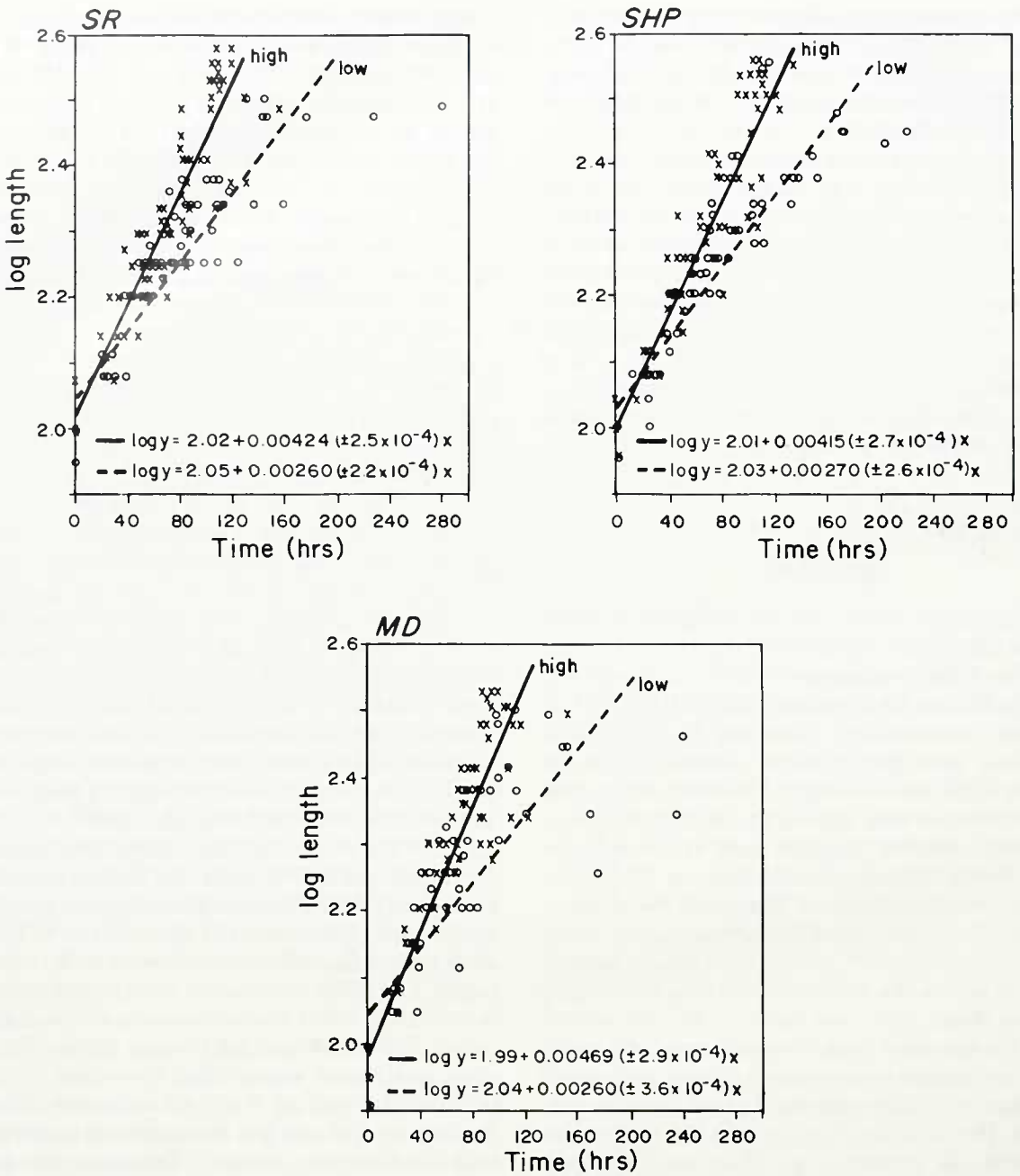

Figure 4. Growth rate ($\log_{10}$ μm h^{-1}) of *Scottolana canadensis* nauplii collected from three locales [Saco River (SR), Sheepscott River (SHP), and Patuxent River (MD)] and reared at 20°C and either 2.5 $\times$ 10^5 cells ml^{-1} (solid lines and x data points) or 0.5 $\times$ 10^5 cells ml^{-1} (dashed lines and O data points). The 95% confidence interval of the slope is provided in the regression equation.

(1985a). The average egg volume from field-collected females ranged from 1.17 to 1.40 $\times$ 10^5 μm^3 when temperatures ranged from about 13 to 18°C (unpubl.).

An alternate hypothesis of the "nauplius development time restriction hypothesis" to explain differences in newborn size of *S. canadensis* is that variation in primary productivity between latitudinally separated locales may be significant (Lonsdale and Levinton, 1985a). In Chesapeake Bay during the spring bloom, the chlorophyll concentration exceeded 40 mg m^{-3} in the euphotic zone and 29–48 mg m^{-3} over the entire water column [Malone *et al.*, 1988. Data were converted from mg m^{-2} by using the average euphotic depth (5 m) or range of channel depths (25–42 m), respectively]. In the Damaris-

cotta River estuary (just northeast of the Sheepscott River estuary), spring bloom chlorophyll concentrations occurred in late February and early to mid-March with a maximum value of 10 $\mu g\, l^{-1}$ (Townsend, 1984). During May and June when *S. canadensis* have been found in high abundance in Maine (Lonsdale and Levinton, 1985a), the chlorophyll values ranged from 4 to 5 $\mu g\, l^{-1}$ (Townsend, 1984). Although chlorophyll concentration *per se* is not always an adequate indicator of food availability (Bellatoni and Peterson, 1987), we suggest that the variation in newborn size found among *S. canadensis* nauplii may reflect differences in food availability between the Maine and MD habitats.

At present, biochemical measurements of genetic variation among and within *S. canadensis* populations are lacking. Despite common-rearing, some of the variation found may not be related to genetic differences, but to other irreversible, non-genetic effects (*e.g.*, maternal effects due to the handling history of individual females within a locale). Ecological studies of the energy demands of copepod nauplii during development and the coupling of primary production to patterns of copepod reproduction and survival in the field would further our understanding of the evolution of life-history strategies of marine invertebrates.

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